

Research Article

Cataloguing the alien spermatophyte flora of a remote tropical island: Methods and insights from Isla del Coco, Costa Rica

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Abstract

Invasive alien species are one of the most severe threats to island biodiversity. An essential first step in addressing this issue is producing comprehensive inventories of alien species inhabiting them. However, cataloguing alien floras on remote islands is particularly challenging. Botanical surveys are often conducted only after substantial human-driven impacts on local ecosystems, including the introduction of invasive species, have already occurred. This raises the key question of how species' native origin should be determined on islands with such a recent history of botanical documentation. Site-based methodologies offer a practical, replicable and context-sensitive approach to addressing these challenging knowledge gaps. Here, we present a comprehensive catalogue of the alien spermatophyte flora of Isla del Coco, an eastern Pacific island located approximately 500 km off the Central American mainland and facing the aforementioned challenges. Among the main contributions of this study, we apply an expert-based binary decision tree to classify the wild flora as native, wild alien, or cryptogenic, along with a separate inventory of cultivated species. Our classification system allowed us to identify 89 wild alien species (45.2% of the island's total wild flora), 78 native species (39.6%), and 30 cryptogenic (15.2%). The naturalised-to-native ratio (0.5) suggests that the island remains highly susceptible to biological invasions. The profile of the alien flora closely resembles that of mainland Central America, with a predominance of unintentionally introduced species, underscoring the need for strict biosecurity measures at landing points. The methodology employed also indicates that site-based approaches may apply stricter criteria for defining native species than previous studies, thereby highlighting new research needs for Isla del Coco, such as clarifying the status of cryptogenic species and investigating the largely unexplored impacts of invasive alien plants.

Key words: Biological invasions, ecology of place, island biogeography, site-based methodologies, species classification, tropical islands



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Introduction

Islands account for only 5.3% of the Earth's land surface, yet they host approximately 31% of all known plant species (Weigelt et al. 2013; Schrader et al. 2024). Moreover, they support 21% of global plant endemism, largely driven by their

geographic isolation, that promotes diversification and speciation (Whittaker et al. 2023). These figures highlight the critical importance of islands as biodiversity hotspots and priority areas for global conservation efforts. Nevertheless, the very features that foster such unique biotas, namely isolation, limited area and ecological fragility, also make island biodiversity particularly vulnerable to anthropogenic global change (Brock and Daehler 2022). Among the most severe threats is the introduction of invasive alien species, which ranks among the four most significant drivers of biodiversity loss across most island systems (Fernández-Palacios et al. 2021). In fact, invasive alien species are involved in approximately 90% of extinctions recorded on islands worldwide (Bacher et al. 2024). Islands with greater isolation, larger area, higher elevation, and locations in the Pacific Ocean tend to support higher richness of alien naturalised species (Pyšek et al. 2017; Essl et al. 2019).

Determining the native origin of plant species in isolated areas (i.e., whether it is native or alien to that area) is inherently challenging because of their limited and/or late botanical exploration. Far from being an exception, this situation is common across most oceanic islands. In fact, there is a worrisome lack of collections from the scattered islands of the Pacific among the world's largest natural history museums and herbaria (Ball et al. 2025). In addition, most floristic surveys of oceanic islands are relatively recent, typically conducted long after large-scale human activities had begun to affect local habitats; for instance, when the first flora of Juan Fernandez Archipelago was compiled (1896) the islands were already seriously deforested (Stuessy 2020). In ecosystems with poorly documented human and natural histories, determining the native origin is particularly difficult. In these cases, site-based methodologies represent a practical and context-sensitive approach for addressing these challenges (Billick and Price 2010); especially when considering that biological invasions are explicitly context-dependent (Pearson 2024). Effective application of such methodologies requires a nuanced understanding of both human activity and natural history, with a focus on introduction pathways and the timing and extent of human influence.

Isla del Coco is Costa Rica's most remote island, located approximately 500 km off the Central American mainland and with only 24 km² surface. It is the only island with tropical rain forests in the Tropical Eastern Pacific realm (Spalding et al. 2007; Claudino-Sales 2019), and its uniqueness has been recognised with the designation of a World Heritage Site in 1997 (UNESCO 1998). The island's topography is highly irregular, with mountains rising up to 575 m a.s.l., which makes it difficult for humans to move across the terrain (Montoya 2008). Most of the island's coastline is bordered by cliffs (Hertleim 1963), with only three topographically accessible areas: Wafer Bay, Chatham Bay, and Yglesias Bay—the latter being largely inaccessible for most of the year due to strong marine currents (Trusty et al. 2006). Despite its small size, Isla del Coco supports remarkable biodiversity, with at least 220 native plant species and 560 native animal species, including 48 endemic plants and 77 endemic animals (Hogue and Miller 1981; Villegas-Retana et al. 2016; Estrada-Chavarría et al. 2020; Viquez 2020; Montoya 2021). The introduction of alien species is considered one of the two main impacts on Isla del Coco, alongside the deforestation for agricultural establishment that occurred during the 19th century (Acosta-Vargas et al. 2020).

Spanish explorers discovered the island in 1526 (Estrada-Chavarría et al. 2020), and in 1546 F. Bernaldo de Quirós made the first documented plant introduction, who allegedly planted some fruiting species brought from Peru (Trusty et

al. 2006). This was followed by several subsequent documented introductions, including those carried out by whalers and crews of scientific expeditions by the late 18th century (Passmore 1895; Pittier 1899; Jinesta 1937). In the 19th century, more than 400 treasure-hunting expeditions took place, likely introducing new species (Montoya 2016). In 1878, a penal colony was established in Chatham Bay, and in 1889, the Cocos Island Agricultural Company made the only attempt at permanent human settlement (Jinesta 1937). This settlement lasted 16 years and involved the cultivation of numerous alien species in both northern bays (Chatham and Wafer bay; Jinesta 1937; Trusty et al. 2006). Since then, the island has remained uninhabited. However, human presence has continued up to the present day. Currently, there are at least 14 buildings in Wafer Bay and a single currently unused building in Chatham Bay. Park rangers, paramedics, volunteers, and researchers work in monthly shifts, with a supply ship transporting the entire crew along with food, fuel, and essential work materials. Some tourist ships operate in the area; however, since their main activity is scuba diving, they typically visit only Wafer or Chatham Bay for a few hours once a week. Agriculturally valuable species are cultivated by park rangers in the northern bays. Prior to 2008, numerous instances of cultivated plant escape were recorded near Wafer Bay. Between 2005 and 2008, ecological restoration actions were implemented, including eradication actions or measures to prevent the escape of cultivated species near human settlements, such as the establishment of a single, clearly defined cultivation area, which has been managed through regular mowing to prevent plant escape, and the implementation of a composting system that treats all organic waste on the island, effectively neutralising seed germination (Madriz 2009). However, the island still lacks biosecurity measures for goods monthly transported from mainland Costa Rica, making the introduction of alien plant species an ongoing concern.

Regarding the early botanical records of Isla del Coco, the first documentations include those by A. Menzies in 1794–1795 (van der Werff 2002; Hammel et al. 2004), G.W. Barclay in 1838 (Belcher 1843; Adams 1992), and G. Bentham between 1836 and 1839 (Bentham et al. 1844), all of whom collected few scattered specimens. Subsequently, some checklists of the island's flora were published: a list of six taxa by Rose (1892), ca. 40 taxa by Pittier (1899), and 38 taxa by Robinson (1902). Later in 1902, Pittier revisited the island (Cortés 2008), although he never published an updated checklist. The earliest relatively complete plant record was compiled by Stewart (1912), who conducted a ten-day specimen collection, surveying most of the island's major habitats—including humid forest, riparian zones, cliffs, bay shore vegetation, and landslide areas. In total, 82 taxa were recorded: 74 at the species level, five at the genus level, and three at the family level. Nevertheless, the eastern part of the island remained unexplored by Stewart, and elevations above 200 m a.s.l. were not reached during that survey. Stewart's work is widely regarded as foundational for defining the native origin of the island's plant species. Subsequent researchers have updated and expanded upon Stewart's work, culminating in the most recent checklist by Estrada-Chavarría et al. (2020).

However, despite these efforts, Isla del Coco still lacks a comprehensive plant inventory that includes an up-to-date and consistent list of alien plant species. Accurate and standardised inventories of alien plant species are essential tools for the effective early detection of new introduced species and a clear understanding of their current state and invasiveness risk (Herrera et al. 2025 and references therein). In this study, we present the first catalogue of the alien spermatophyte flora

of Isla del Coco, including invasion status categories. Additionally, we provide ecological profiles and invasion risk indicators to offer a comprehensive assessment of the current situation and possible future scenarios regarding alien species on Isla del Coco. Lastly, we reflect on the methodological approach used, outlining key considerations and lessons learned for future assessments in similarly under-documented island ecosystems.

Methods

Study area

Isla del Coco is a volcanic island located between the Costa Rican mainland and the Galapagos Archipelago, 492 km and 781 km away, respectively (Fig. 1); its coordinates are 5°30'–5°34'N and 87°01'–87°06'W. This isolated island is the only emergent point of the Cocos Ridge, a submarine mountain range on the Cocos Plate (Claudino-Sales 2019). The island covers an area of 24 km², measuring approximately 7.6 km from northeast to southwest and 4.4 km from northwest to southeast (Montoya 2016; FAICO 2025). Its topography is rugged, with steep valleys and dramatic sea cliffs surrounding nearly the entire coastline (Pittier 1899; Jinesta 1937; Trusty et al. 2006). The highest point is Cerro Yglesias, reaching 575 m a.s.l. (Montoya 2016). The mean annual temperature is 24.6 °C, and average annual precipitation reaches an impressive 5000 mm, due to the island's location within the Intertropical Convergence Zone (Alfaro 2008). According to Holdridge's life zone classification, the island is categorised as premontane rain forest below 300 m a.s.l., and montane rain forest above this elevation (Porrás-Jiménez et al. 2014).

Like most isolated oceanic islands, Isla del Coco has a rich flora (220 native plant species; Estrada-Chavarría et al. 2020), which becomes more evident if we compare it with that of the neighbouring Galapagos Archipelago (552 native plant species in a much larger area of about 8000 km²; Tye 2006). Although the overall endemism rate of Isla del Coco is modest (22%), it exhibits an exceptional diversity of lycophytes and ferns, which account for 47% of the native flora and 60% of the endemic species—an unparalleled pattern among oceanic islands (Trusty et al. 2006). These authors identified seven vegetation types on the island: (1) low elevation humid forest, which corresponds to Holdridge's premontane rain forest, dominates the landscape and features a low-diversity canopy of *Sacoglottis holdridgei* (endemic), *Clusia rosea*, and *Ocotea insularis*, with a dense understory of Melastomataceae, endemic tree ferns, and abundant epiphytes; (2) high elevation cloud forest, which corresponds to Holdridge's montane rain forest, has a homogeneous canopy of *S. holdridgei* and an understory dominated by *Cyathea alfonisiana* (endemic) and dense moss carpet; (3) riparian areas, similar in composition to the low elevation humid forest but with additional understory species such as *Spathiphyllum laeve* and *Danaea nodosa*; (4) bay shore vegetation, dominated by *Hibiscus tiliaceus* subsp. *pernambucensis*, with *Mucuna sloanei*, *M. mutisiana*, and *Canavalia maritima* vines; (5) coastal cliffs, primarily covered by *Cecropia pittieri* (endemic) and *Clusia rosea*, with dense *Ipomoea* spp. vines; (6) landslide areas, colonised first by the creeping ferns *Dicranopteris flexuosa* and *Gleichenella pectinata*, and after by *Cecropia pittieri*; and (7) the small islets surrounding Isla del Coco, which are primarily covered by *Chloris paniculata* (endemic).

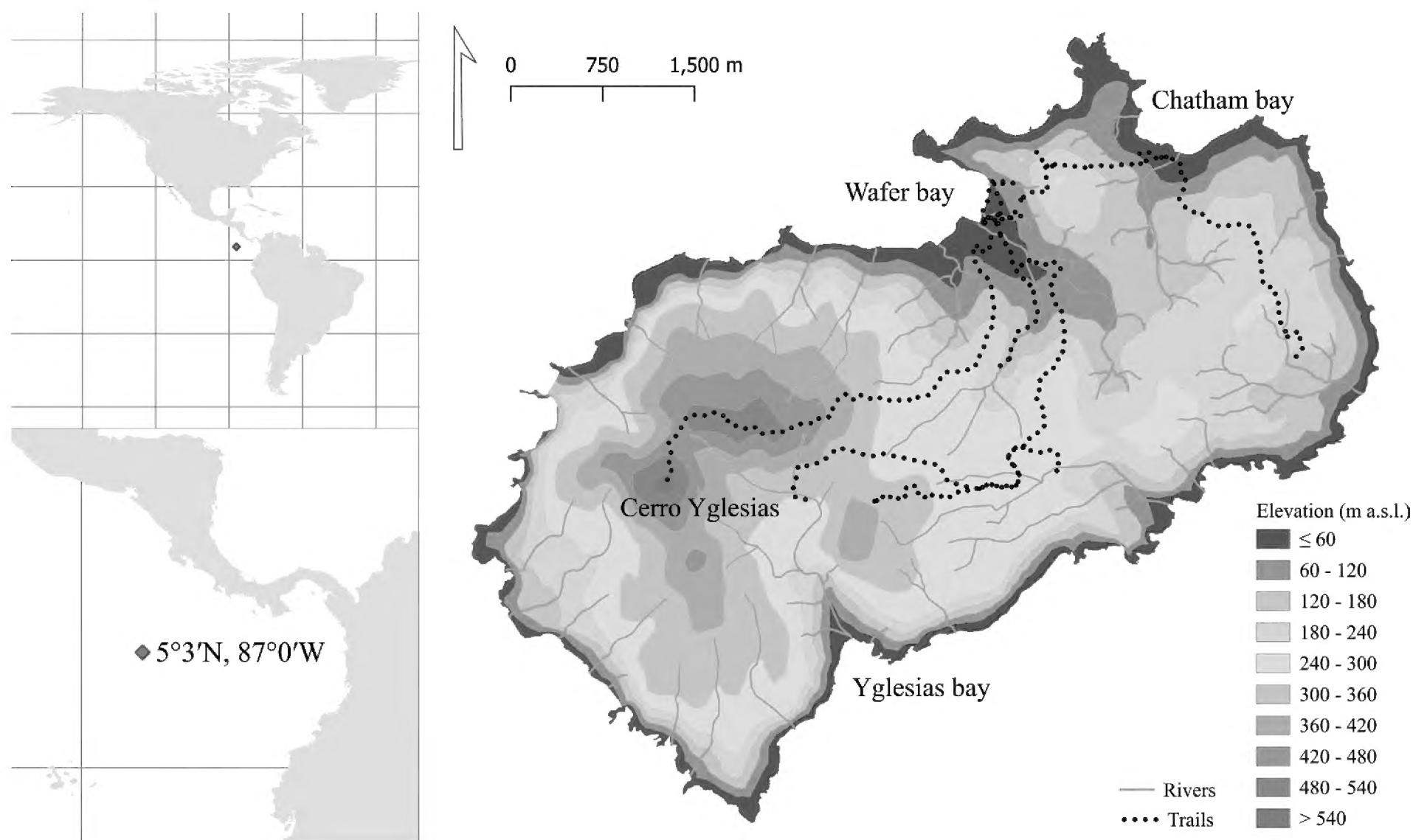


Figure 1. Geographic location of Isla del Coco. The top left inset shows its position relative to the continent, and the bottom left inset shows its location within Central America. The main hypsometric map (right) displays the island with its bays, hills, rivers and trails.

Regarding the island's fauna, invertebrates are highly diverse, with 346 insect species recorded, including 63 endemics (Hogue and Miller 1981), along with 50 arachnids that include 10 endemics (Viquez 2020). Vertebrates are represented by 142 non-breeding migrant bird species, and 14 resident bird species, of which three are endemic (Montoya 2021), as well as three reptile species—two endemic and one introduced (Villegas-Retana et al. 2016). Although there are no native amphibians or mammals on the island, five invasive alien mammals are present—feral pigs (*Sus scrofa*), white-tailed deer (*Odocoileus virginianus*), domestic cats (*Felis catus*), and two rat species (*Rattus rattus* and *Rattus norvegicus*) (SINAC 2017). Both *Sus scrofa*'s and *Odocoileus virginianus*'s estimated population densities are 19.2 and 2.1 individuals per square kilometer, respectively (SINAC 2020).

Data sources and taxonomic backbone

To build an inventory of alien spermatophyte species, we first compiled a comprehensive list of all known spermatophyte species in the island. The checklists by Trusty et al. (2006) and Estrada-Chavarría et al. (2020) served as the foundation for this database, which was later supplemented with fieldwork and historical testimonies (Pittier 1899; Jinesta 1937). Each species was verified using herbarium specimens, photographic records, or written testimonies (the latter accepted only for unmistakable taxa, i.e., crops). The herbarium specimens were consulted in the websites of the California Academy of Sciences Herbarium (CAS), Fairchild Tropical Botanic Garden Herbarium (FTG), Gray Herbarium, Harvard University (GH), Missouri Botanical Garden Herbarium (MO), National Herbarium of Costa Rica (CR), United States National Herbarium, Smithsonian Institution (US),

and Herbario Luis A. Fournier, University of Costa Rica (USJ). Cultivated plants without documented instances of escape were not included in the wild alien plant inventory, although a separate checklist of cultivated species without evidence of escape (hereafter, cultivated species) is provided. Fieldwork involved the collection of plant specimens and photographic records conducted in 2005–2008 by P. Madriz and in 2024 by B. Orbea, with all specimens deposited at the National Herbarium of Costa Rica (CR). The main effort focused on verifying the presence of alien species around human settlements and along established trails. The low elevation rain forest and high elevation cloud forests were explored with the aim of detecting alien species, by following the main paths and making short perpendicular incursions from the trail. The presence of alien species was also verified in bay shore vegetation (Wafer and Chatham), riparian zones (Río Genio and Río Minuto), and cliff zones—though only in the most accessible areas of Wafer Bay. Recent landslide zones, offshore islets, and the southern parts of the island could not be surveyed. The Catalogue of Life (Catalogue of Life Foundation 2025) served as the taxonomic standard; we standardised all species names by synonymising every record against the Catalogue of Life using the R package *taxize* (Chamberlain and Szöcs 2013). For angiosperms, family circumscription followed the APG IV system (The Angiosperm Phylogeny Group 2016). There are no known gymnosperms on the island.

Inventory of wild alien species

Our initial methodology was based on native versus alien status information provided in previous checklists. However, upon comparing the most recent lists and their criteria for identifying alien species, we recognised the need to develop a replicable, site-based framework for distinguishing between native and alien plants. Previous checklists, such as those by Trusty et al. (2006) and Estrada-Chavarría et al. (2020), classify as alien any ruderal species not documented in Stewart (1912). However, it overlooks key factors such as the native range of species and the island's specific human–environment dynamics. Consequently, alien species introduced prior to 1912 and non-ruderal species introduced later would be incorrectly treated as native, representing some of the potential classification errors that may arise. While the foundations of this method are logical, they are insufficient on their own and require complementary considerations to accurately determine the native origin of species on the island.

To address this, we developed a binary decision tree based on seven guiding questions (Fig. 2) and applied it to all spermatophyte taxa. The decision tree categorises species into three groups (native, wild alien, and cryptogenic). The first five questions of the decision tree focus on (i) the species' endemism [Question 1 (Q1)]; (ii) native range (whether the species is native or alien to the Neotropics; Q2); (iii) presence in the earliest comprehensive botanical documentation of the island (Stewart 1912) or earlier testimonies (Q3); (iv) ruderal and/or useful for humans elsewhere (Q4); and (v) ruderal behaviour on Isla del Coco (Q5). Q1 was answered using the latest checklist (Estrada-Chavarría et al. 2020). Q2 was addressed using data from Germplasm Resources Information Network, GRIN (USDA 2025a) and Plants of the World Online, POWO (2025). Q3 was resolved based on Stewart (1912) or earlier testimonies. Q4 was answered consulting terms such as 'roadsides', 'road edges', 'disturbed areas', 'highways', 'fields', 'grasslands', 'plantations', 'crops', 'gardens' or 'cultivated' in the species descriptions of the "Manual de Plantas de Costa Rica"

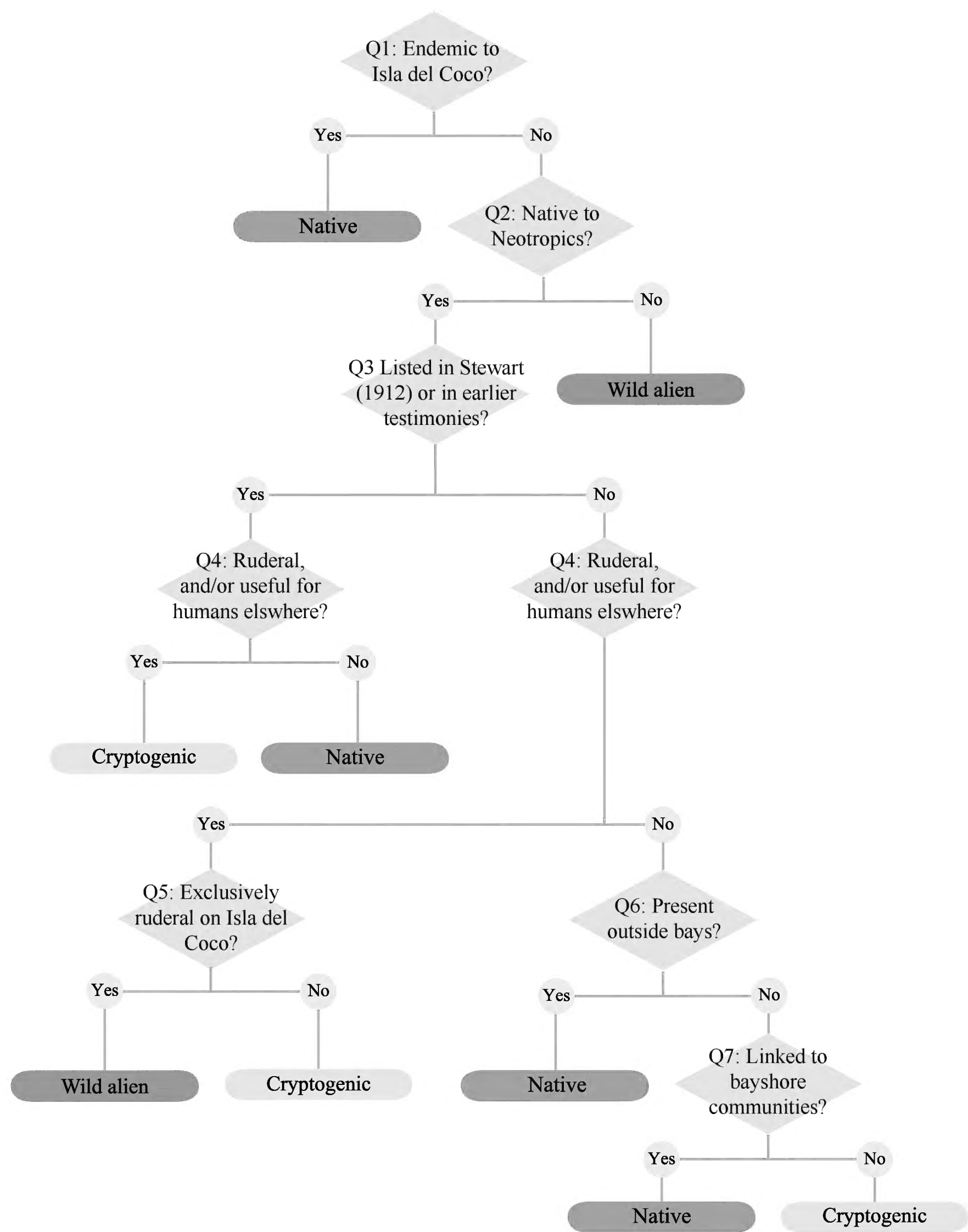


Figure 2. Binary decision tree for determining the native origin of spermatophyte species on Isla del Coco. Taxa were systematically subjected to a series of questions until they were assigned to one of the following categories: native, cryptogenic, or alien.

(Hammel et al. 2003–2015) and the “Flora de Nicaragua” (Stevens et al. 2001) or, for species not covered in these floras, Tropicos database (Missouri Botanical Garden 2025). Q5 was addressed with fieldwork and herbarium voucher locations. This combination of native range, early botanical records, and distinctions between ruderal or non-ruderal plant presence provides a robust framework for determining the native origin of species in areas with limited botanical documentation.

Unlike questions 1 to 5, which focus on plant species, the last two questions (Q6 and Q7; Fig. 2) address specific human–environment dynamics on Isla del Coco. As noted above, the island’s geomorphology and human activity are shaped by the fact that only its northern bays are accessible, while the rest of the coastline is bordered by steep cliffs. As a result, human settlements overlap spatially with bay shore vegetation (Trusty et al. 2006). These site-specific conditions create unique human–environment interactions, generating areas where the introduction pathways of alien species coincide with the bay shore vegetation. Therefore, species found only in Wafer and Chatham bays may be present either due to human introduction or because of specific habitat requirements. Consequently, the last two questions focus on this particular situation, where the classification of a species as native, alien, or cryptogenic is inferred from its presence beyond the bays (Q6) and its ecological dependence to bay shore vegetation (Q7). Q6 was answered with fieldwork and herbarium voucher locations and Q7 by consulting habitat descriptions in the “Manual de Plantas de Costa Rica” (Hammel et al. 2003–2015) and the “Flora de Nicaragua” (Stevens et al. 2001), or, for species not covered in these floras, Tropicos database (Missouri Botanical Garden 2025).

As a result of this classification system, every species is assigned to one of three categories: native, wild alien, or cryptogenic. Native taxa are those that have originated in a given area without human involvement or have arrived there without intentional or unintentional human intervention from areas where they are native (Pyšek et al. 2004). Wild alien taxa, a subset of alien taxa by Pyšek et al. (2004), are those that have arrived to a given area by intervention of humans, either intentionally or accidentally, and have established populations outside cultivation, with records of spontaneous escapes or naturalised populations in the wild. The cryptogenic category includes species whose origin in a particular area is uncertain—where it remains unclear whether they are truly native or alien (Carlton 1996).

The wild alien plant species compiled in our inventory were assigned an invasion status category following the framework proposed by Pyšek et al. (2004). Casual alien species are those that may grow and occasionally reproduce outside cultivation but do not form self-replacing populations and often depend on repeated introductions to persist. Naturalised species are alien plants that maintain self-replacing populations for at least 10 years without direct human intervention, reproducing through seeds or vegetative structures capable of independent growth. Invasive species are a subset of naturalised plants that produce reproductive offspring—often in large numbers—at considerable distances from parent plants, with the potential to spread widely. As detailed data on the spread rates and ecological impacts of naturalised species in this region are lacking, we classify all naturalised species with clear evidence of displacing native vegetation as invasive, according to expert criteria. These cases involve alien species forming dense stands, becoming locally dominant, and reducing the presence of other native flora (see Suppl. material 1).

Between 2005 and 2008, an ecological restoration plan was implemented, together with the establishment of various biosecurity measures (Madriz 2009). We include the category ‘eradicated’ for species that were specifically targeted during eradication efforts of the ecological restoration plan and have not been observed since. Additionally, we highlight species for which no records have been documented since 2008, either in herbaria or in the field, even if they were not specifically targeted for eradication.

Alien species ecological profile: native range, life form, and reason for introduction

The native range of each species was defined according to the eight biogeographic realms proposed by Udvardy (1975): Nearctic (North America, Greenland), Neotropical (Central and South America, the Caribbean, southern Florida), Palearctic (Europe, northern Africa, northern and central Asia), Afrotropical (Sub-Saharan Africa, Madagascar, Arabia), Indomalayan (India, Southeast Asia, southern China), Australasian (Australia, New Guinea, Tasmania), Oceanian (Central and South Pacific islands), and Antarctic (Antarctica, Subantarctic Islands). In cases where a species is primarily distributed on a single biogeographic realm and only marginally on a second one, we consider only the primary realm. Data on the native range of each species was extracted from GRIN (USDA 2025a) and POWO (2025). In cases of disagreement, we only considered realms on which both sources agreed.

Life forms were defined according to the seven categories proposed by Engemann et al. (2016): epiphyte, liana, vine, herb, shrub, tree, parasite, or aquatic. The data were taken from the Engemann et al. (2016) dataset; for plant species not included in this dataset, we replicated their classification workflow using BIEN (Maitner et al. 2017), TRY (2025), PLANTS Database (USDA 2025b), and Tropicos database (Missouri Botanical Garden 2025). Additionally, lifespan information for each species (i.e., whether they are annual or perennial) was obtained from PLANTS Database (USDA 2025b). Regarding the reason for introduction, the following use categories were considered: accidental, human food, medicinal, ornamental or animal food. We obtained the uses of each species from GRIN (USDA 2025a).

Distribution, abundance and invasiveness risk assessment

The species distribution was categorised as either punctual or scattered. Species observed in only one or two sites were considered punctual, while those found in three or more sites were classified as scattered. Each of the bays and trails was considered an independent site: Wafer Bay, Chatham Bay, the trail between Wafer and Chatham, the trail to Los Llanos, the trail to Catarata Río Genio, and the trail to Cerro Yglesias. Observations made in areas far from bays and trails—meaning in undisturbed ecosystems—were treated as an additional site. At first, we considered dividing these undisturbed areas into separate sites; however, we ultimately retained them as a single unit, since most wild alien species were closely associated with human disturbance and were rarely found outside disturbed areas. We used herbarium records and field observations to confirm the presence of species at each site. Regarding abundance, each species was classified as either scarce or abundant based primarily on expert criteria during fieldwork. We also considered qualitative information on relative abundance found in herbarium records. Whenever a species could not be observed in the field, or when there was a discrepancy between herbarium data and field observations, we did not assign an abundance category.

For the invasiveness risk assessment, we used the global risk score from the “Global Compendium of Weeds” (Randall 2017). This scoring system allows us to classify the global invasiveness risk of a given species into four categories: extreme, high, medium, and low based on its interactions with humans and its documented global behaviour, aligning with research that identifies a species’ history of being a weed elsewhere as the most reliable predictor of its potential weediness. The

assessment is based on three main criteria: (1) the species’ ability to enter new environments, (2) its capacity to spread and establish over wider areas through various dispersal mechanisms, and (3) its ecological impacts in those environments (Randall 2017). We conducted a Fisher’s exact test to corroborate the relationship between the global risk score (extreme, high, medium, and low) and the invasion status (casual, naturalised and invasive) using R software.

Inventory of cultivated plants

As mentioned above, we excluded from the inventory of wild alien species those non-escaped alien species that were cultivated on Isla del Coco. However, to ensure comprehensive records we compiled a separate inventory of cultivated species, which includes both current and historical records of cultivation. This serves as a precautionary measure, establishing a precedent for their presence in case these species escape into the wild in the future. For each species in this inventory, we include the state of cultivation as either actively cultivated or no longer cultivated. Following the methodology described earlier, we also included its ecological profile and global risk score, in order to support future monitoring and risk assessment efforts.

Results

Overview of the inventory of wild alien species

Our work provides the most consistent inventory of wild alien species on Isla del Coco to date (see Suppl. material 2). A total of 197 wild spermatophyte species, belonging to 144 genera and 59 families, were assessed for classification (see Suppl. material 3). Nine species were excluded due to doubtful records (*Eleocharis mutata*, *Melinis minutiflora* and *Vigna vexillata*) or because they could not be identified to species level (*Crescentia* sp., *Freziera* sp., *Hedyosmum* sp., *Ilex* sp.1, *Ilex* sp.2 and *Palicourea* sp.). Another 34 species were excluded but categorised as cultivated (see below). Our classification (Table 1 and Fig. 3) identified 89 wild alien species (i.e., 45.2% of the island’s total wild flora), 78 native species (39.6%), and 30 cryp-

Table 1. Definitions of categories used to classify the alien flora of Isla del Coco in the present study. The number of species and families corresponding to each category is indicated on the right.

Cathegory	Definition	Species	Families
Native	Taxa that are originated in a given area without human involvement or that arrive there without intentional or unintentional human intervention from an area in which they are native (Pysek et al. 2004).	78	36
Cryptogenic	Taxa in a given area whose origin is uncertain due to unclear human involvement; they are not demonstrably native or alien (Carlton 1996).	30	14
Alien	Taxa in a given area that are introduced due to intentional or unintentional human involvement, or that arrive from areas where they are alien (Pysek et al. 2004).	123	49
Cultivated	Alien taxa that arrive through intentional human intervention and have never established populations outside cultivation, with no records in the wild.	34	19
Wild alien	Alien taxa that arrive through human intervention, either intentional or unintentional, and have established populations outside cultivation, with records of spontaneous escapes or naturalised populations in the wild.	89	42
Casual	Wild alien taxa that may flourish and occasionally reproduce outside cultivation, but that eventually die out because they do not form self-replacing populations and rely on repeated introductions for their persistence (Pysek et al. 2004).	48	30
Naturalized	Wild alien taxa that sustain self-replacing populations for at least 10 years without direct human intervention by recruitment from seed or ramets capable of independent growth (Pysek et al. 2004).	34	16
Invasive	Naturalised taxa that form dense thickets and displace native vegetation.	5	5

togenic species (15.2%). Regarding the invasion status of the wild alien species, we identified 48 casual species, 34 naturalised species, and five invasive species, while two species remained unclassified. Cyperaceae and Poaceae dominated both alien flora (11.2% and 10.1%, respectively) and naturalised species (23.5% and 17.6%), whereas Fabaceae (10.4%) and Solanaceae (6.2%) predominated among casual species (Fig. 4). The invasive species were *Calophyllum inophyllum*, *Coffea arabica*, *Megathyrsus maximus*, *Terminalia catappa*, and *Urena lobata*.

Alien species ecological profile: native range, life form and reason of introduction

All alien plant species on Isla de Coco had a tropical realm as part of their native range (Fig. 5). The Neotropics were by far the most common native range, followed by the Indomalayan realm. As shown in the vertical bars of Fig. 5, 55.1% of all wild alien species were exclusive to the Neotropics. This proportion was 66.7% among casual species, 41.2% among naturalised species, and 20.0% among invasive species.

The growth forms of alien taxa on the island were represented by herbs (64.0%), trees (22.5%), shrubs (9.0%), and vines (4.5%). No epiphytes, lianas, parasites,

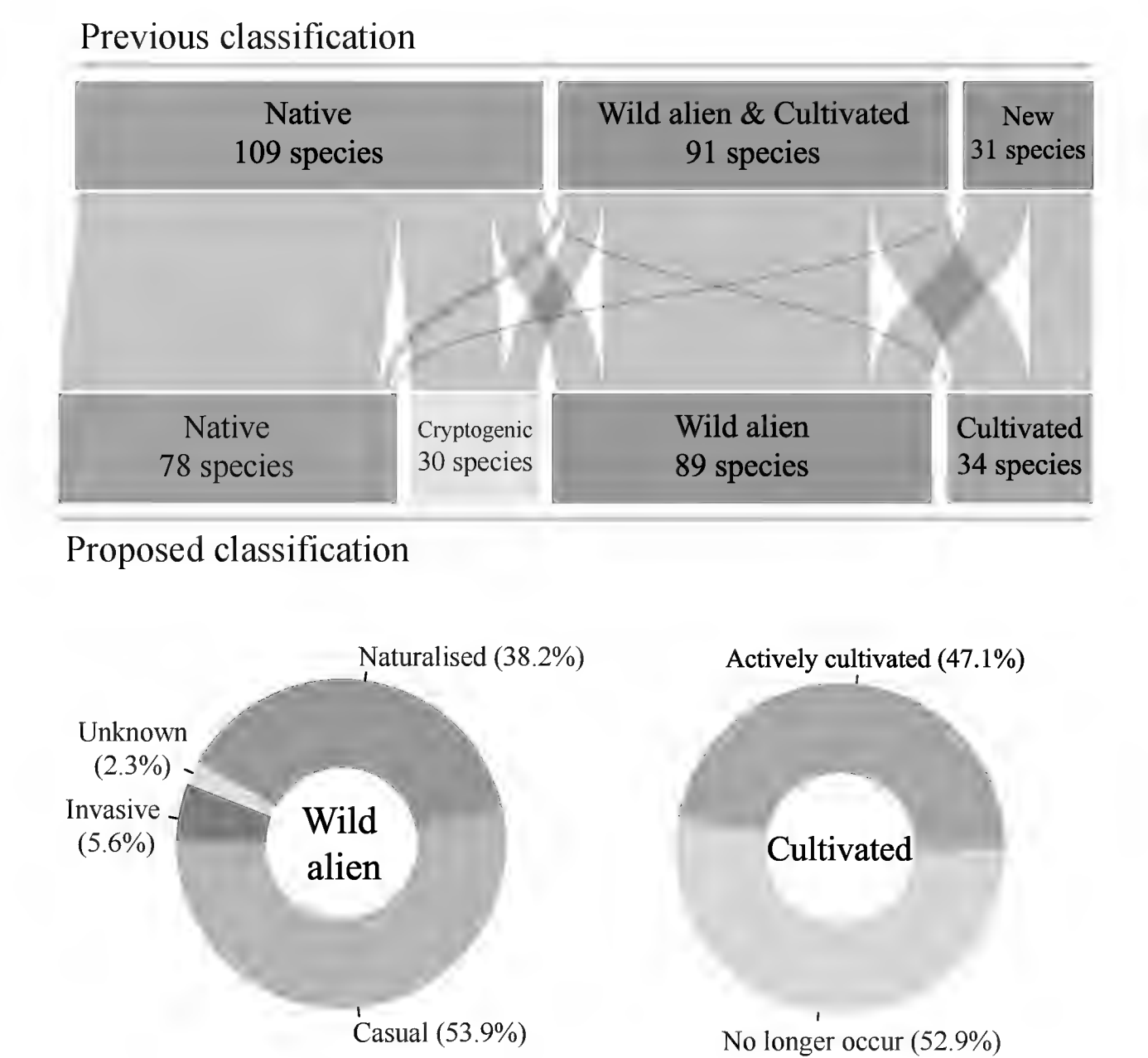


Figure 3. Reclassification of the native origin categories of species on Isla del Coco. Above: Sankey diagram showing the reclassification of categories. The previous classification (upper section) combines the criteria of Estrada-Chavarría et al. (2020) and Trusty et al. (2006), giving priority to the former in case of discrepancy. Wild alien species and cultivated species from previous classifications are grouped together here, since no clear distinction has been made regarding their escape from cultivation. The proposed classification (lower section) results from the binary decision tree. Below: two pie charts showing the invasion status categories of wild alien plants and the categories of cultivated species.

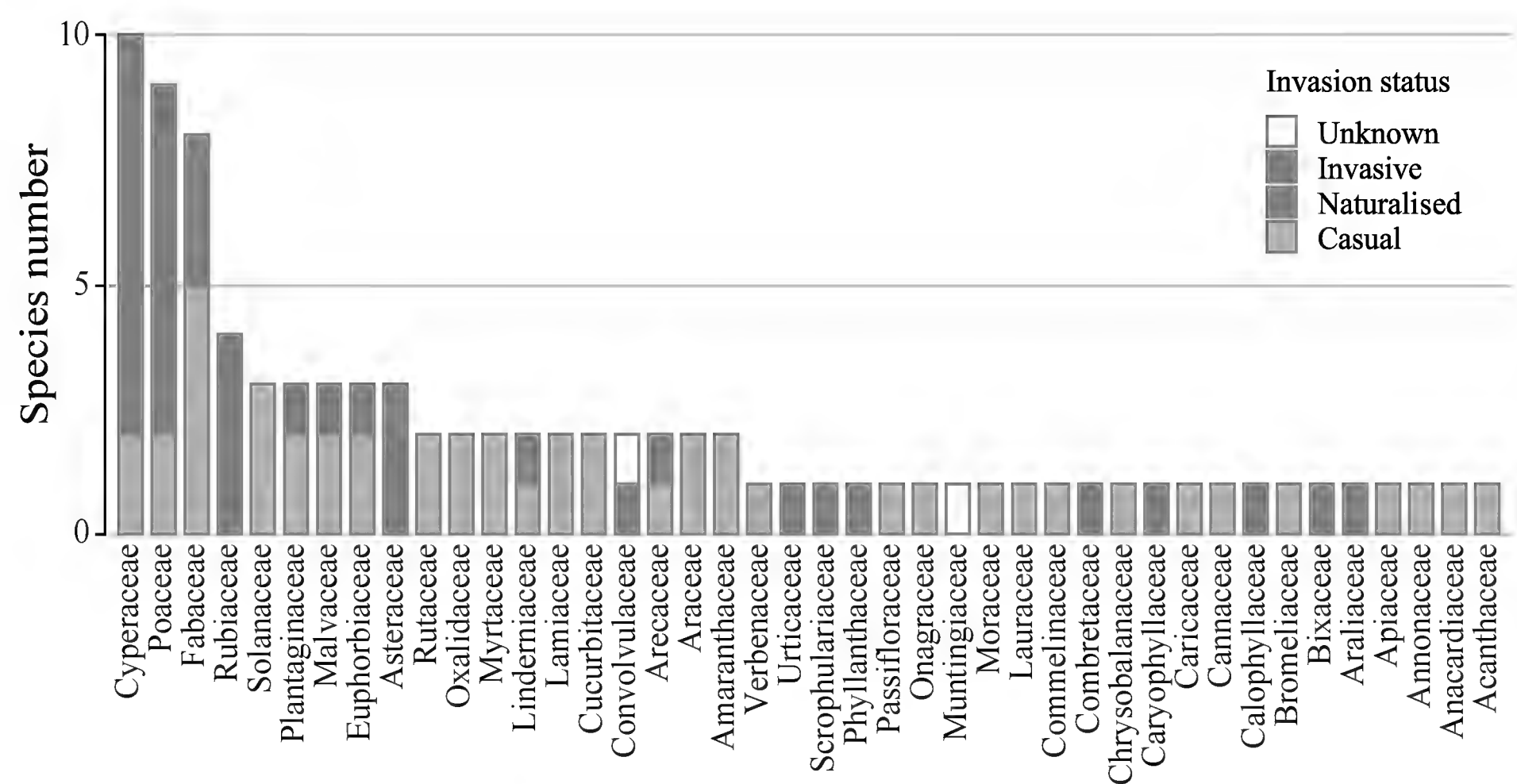


Figure 4. Bar plot showing the families of the wild alien species for Isla del Coco.

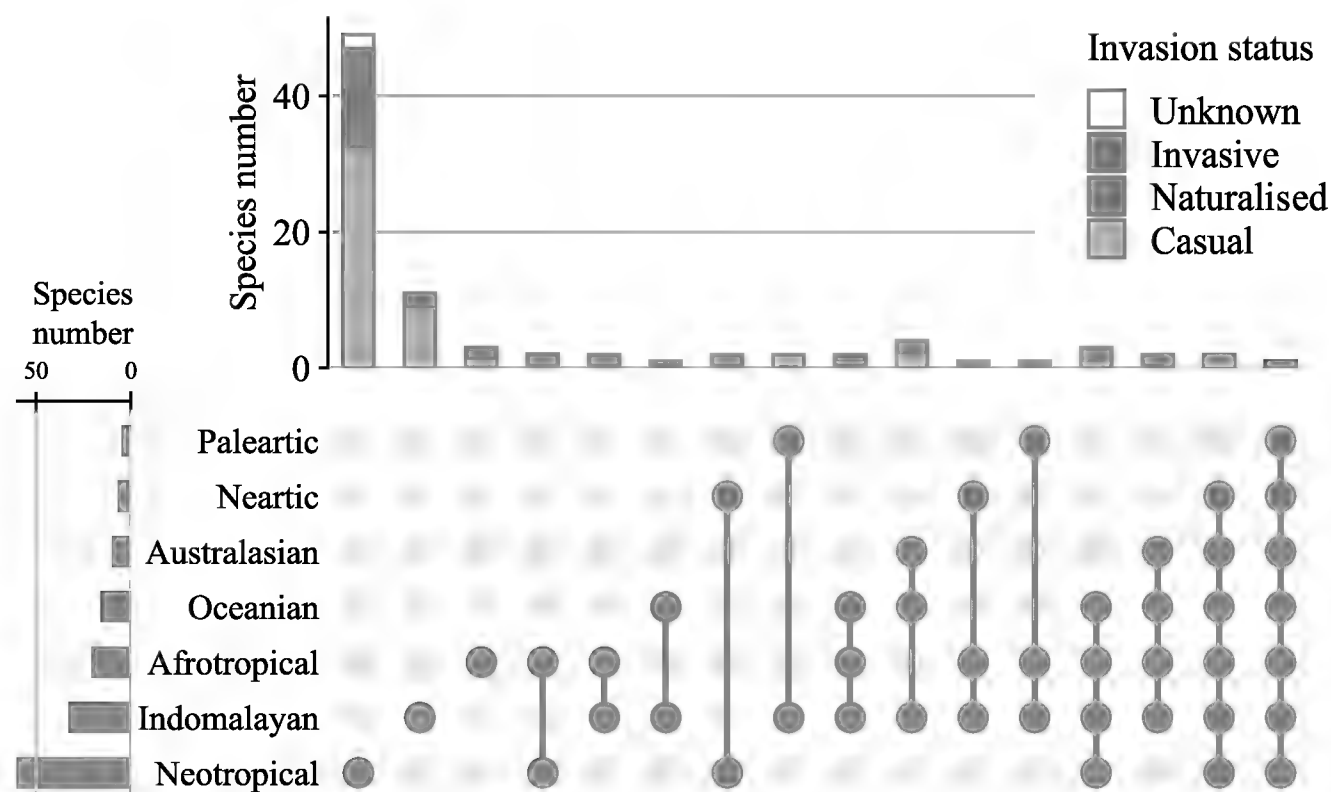


Figure 5. Bar plot showing the native range of wild alien species on Isla del Coco. Vertical bars represent the number of wild alien species that are native to specific combinations of biogeographic realms. Horizontal bars show the total number of wild alien species native to each individual realm, regardless of whether they are also native to other realms.

or aquatic plants were recorded. Herbs and trees were the most common among casual species (58.3% and 29.2%, respectively), while herbs dominated among naturalised species (82.3%). Among invasive species, trees and shrubs were the most represented (40.0% each). Regarding lifespan, herbs comprised 42.1% perennials, 24.6% annuals, and 33.3% that can be either annual or perennial. Vines were 75.0% perennial and 25.0% annual. Trees and shrubs were entirely perennial.

By examining the globally attributed uses of the wild alien plant species of Isla del Coco, we could infer how many were introduced either accidentally or deliberately. A total of 38.2% of these alien species had no known human use, suggesting that they were accidentally introduced into the island. The remaining 61.8% of the species had some known use, with medicinal purposes being the

most common—33.7% when combined with other uses, and 14.6% used exclusively for medicinal purposes. However, most of the species described as having medicinal properties elsewhere in the world are not actually used medicinally on Isla del Coco, so the accidental introductions may be considerably higher than the estimated 38.2%. The second most common category was human food, representing 32.6% of all alien species when combined with other uses, and 12.4% when human food was their sole use. About 11.2% of the species had uses as animal food, with 6.7% having this as their only known use—likely introduced during human settlement attempts in the late 19th century. Finally, 16.8% of the species showed uses for ornamental purposes, although only 4.5% were exclusively ornamental.

Distribution, abundance and invasiveness risk assessment

Regarding distribution patterns, seven species could not be classified into any category because they were not observed in the field. Of the 88 species that could be classified, 75.0% were punctual (found in only one or two locations), while 25.0% were scattered across more than two sites (Fig. 6). When considering invasion status within these spatial patterns, we find that punctual species were mostly casual (68.2%), followed by naturalised (25.8%), invasive (4.5%) and unknown (1.5%). The invasive taxa found in only one or two sites included *Calophyllum inophyllum*, *Megathyrus maximus*, and *Terminalia catappa*, which were confined to the bays. On the other hand, scattered species were predominantly naturalised (77.3%), followed by casual (13.6%) and invasive (9.1%) species.

In terms of abundance, four species were not categorised because they were not observed in the field, or their abundance showed discrepancies with herbarium records. Of the 85 species with abundance category, 83.5% were scarce (64.8% casual and 35.2% naturalised), and 16.5% were abundant—57.1% naturalised, 35.7% invasive and 7.2% casual (Fig. 6).

According to the global risk score, 16 species were classified as low risk, 22 as medium risk, 19 as high risk, and three as extreme invasion risk. Additionally, 29 species remained unscored due to a lack of available data. When comparing these global risk classifications with the observed invasion status on Isla del Coco, Fisher's exact test indicated no significant association ($p > 0.05$).

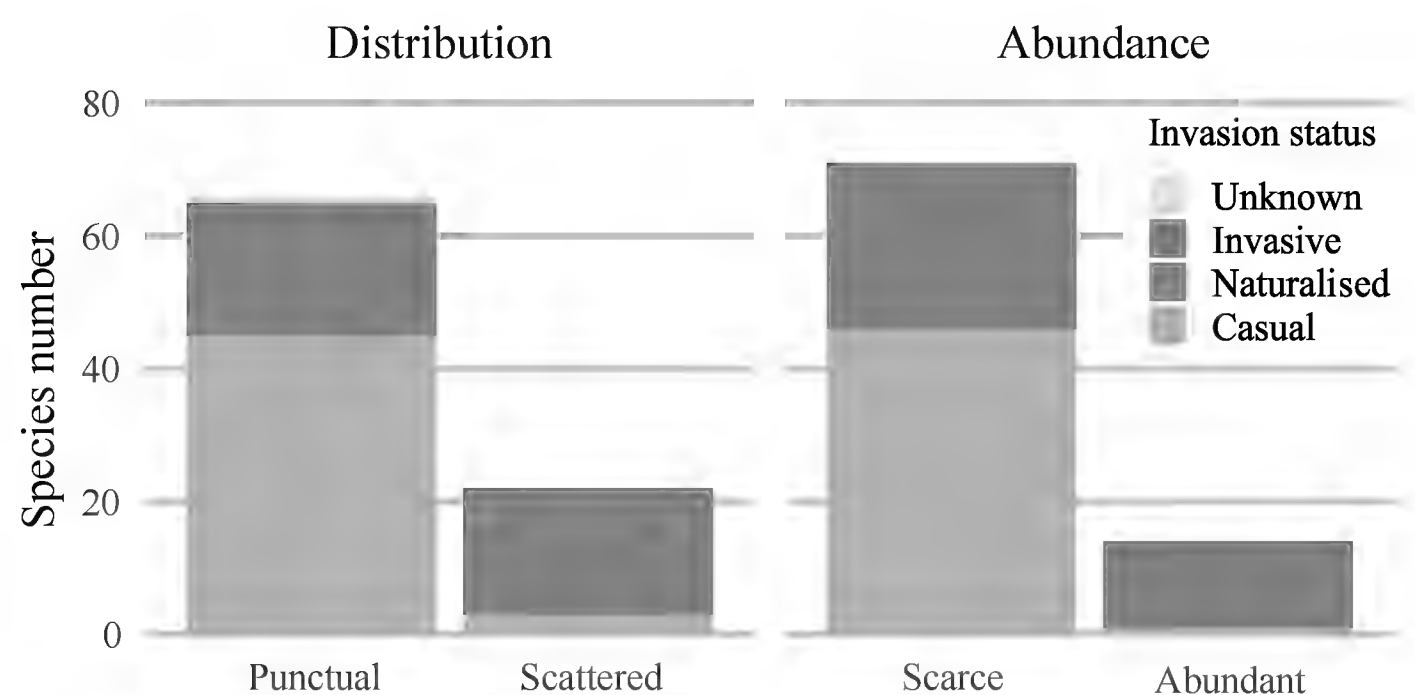


Figure 6. Bar plot showing the distribution and abundance of wild alien species on Isla del Coco.

Cultivated plants

Cultivated species were represented by 34 taxa belonging to 19 families (see Suppl. material 4). Lamiaceae was the family with most species, mainly originating from the Palearctic region. Currently, 18 out of 34 taxa (52.9%) were no longer cultivated on Isla del Coco. Up to 16 taxa (47.1%) were actively cultivated, most of them within the designated cultivation area—except for *Musa acuminata* and *Musa × paradisiaca*, which grow outside of it. Regarding their invasiveness risk assessment, most cultivated taxa (30) fell into the unscored, low, or medium risk categories; only three species were classified as high risk (*Anacardium occidentale*, *Momordica charantia* and *Nicotiana tabacum*) and one as extreme (*Ricinus communis*), but none of these currently occur on the island.

Discussion

Overview of wild alien species of Isla del Coco

Although the total number of wild alien species for Isla del Coco may seem small (89; 48 of them being casual, 34 naturalised and five invasive species), it should be regarded at least as moderate, given its size of 24 km², when compared with other oceanic islands from the eastern Pacific (Table 2). The Revillagigedo Islands (ca. 700 km west of the Mexican coast), with 158 km², host just 81 wild alien plant species (Domínguez-Meneses et al. 2023). The four islands with data on their alien flora of Galapagos Archipelago have a larger amount, but these islands are much bigger than Isla del Coco: Floreana has 203 wild alien species in 173 km², Isabela 407 species in 4586 km², Santa Cruz 576 species in 986 km², and San Cristobal 603 species in 558 km² (Guézou et al. 2010). Although only data on naturalised plants are available, numbers for oceanic islands of the south-east Pacific—very well-known hotspots of invasions (Castro et al. 2007)—do not seem much higher; e.g., in Alejandro Selkirk 126 naturalised species in 48 km², in Rapa Nui 157 naturalised species in 164 km², and in Robinson Crusoe 282 naturalised species in 50 km² (Cáceres-Polgrossi et al. 2023).

The moderate levels of alien plants detected for Isla del Coco align with our expectations, as the island exhibits several traits known to favour the introduction and establishment of alien species in islands worldwide, including isolation (Pyšek et al. 2017), high elevation (Essl et al. 2019), and location in the Pacific Ocean (van Kleunen et al. 2015; Essl et al. 2019). Nevertheless, some characteristics of Isla del Coco may have limited the extent of plant invasions, such as its small area (Pyšek et al. 2017; Essl et al. 2019) and relatively low levels of human-mediated propagule pressure. Human-mediated propagule pressure is a key driver of invasion success; and alien species richness is clearly correlated with levels of human activity both in island and non-island environments (Pyšek et al. 2010; Saccaggi et al. 2021; Vedder et al. 2021). Another factor that may help prevent biological invasions is the island's tropical ecosystems, which have traditionally been considered less invadable than temperate ones—an assumption often attributed to their generally high native species richness (Ackerman et al. 2017). This assumption, however, is only weakly supported and may reflect limited research rather than true ecological resistance (Stadler et al. 2000; Chong et al. 2021; but see Beaury et al. 2020).

Table 2. Native, alien, wild alien, naturalised, casual, and cultivated species, along with their densities relative to land area and the naturalised to native species ratio, for various islands and/or archipelagos across the Eastern Pacific Ocean. *Note: Naturalised species include invasive species. **The area refers to the four largest islands where the study was conducted, not the entire Galapagos Archipelago.

Island	Surface (km²)	Native	Native/km²	Alien	Alien/km²	Wild alien	Wild alien/km²	Naturalised* alien	Naturalised alien/km²	Naturalised to native ratio	Casual alien	Casual alien/km²	Cultivated alien	Cultivated alien /km²	Source
Isla del Coco	24	78	3,25	123	5,13	89	3,71	39	1,63	0,50	48	2,00	34	1,42	Present study
Revillagigedo Islands	158	166	1,05	106	0,67	81	0,51	67	0,42	0,40	14	0,09	25	0,16	Domínguez-Meneses et al. 2023
Galapagos Archipelago	6303**	552	0,09	754	0,12	-	-	264	0,04	0,59	-	-	490	0,08	Guézou et al. 2010
Isalabela	4586	-	-	407	0,09	-	-	179	0,04	-	-	-	-	-	Guézou et al. 2010
Florena	173	-	-	203	1,17	-	-	89	0,51	-	-	-	-	-	Guézou et al. 2010
Santa Cruz	986	-	-	576	0,58	-	-	201	0,20	-	-	-	-	-	Guézou et al. 2010
San Cristobal	558	-	-	603	1,08	-	-	217	0,39	-	-	-	-	-	Guézou et al. 2010
Alejandro Selkirk	48	127	2,65	-	-	-	-	126	2,63	0,99	-	-	-	-	Cáceres-Polgrossi et al. 2023
Rapa Nui	164	50	0,30	-	-	-	-	157	0,96	3,14	-	-	-	-	Cáceres-Polgrossi et al. 2023
Robinson Crusoe	50	147	2,94	-	-	-	-	282	5,64	1,92	-	-	-	-	Cáceres-Polgrossi et al. 2023

Our results show that 43.8% of the wild alien plants in Isla del Coco are naturalised [all ratios presented herein include invasive species within the naturalised category]. Naturalised-to-native species ratio for the island is 0.5 (or 0.36 if cryptogenic are included within the natives). Globally, oceanic islands exhibit a mean naturalised-to-native ratio of 0.84 ± 1.06 (Essl et al. 2019). From this perspective, Isla del Coco falls below the global average in terms of alien species establishment on oceanic islands, despite meeting most of the environmental characteristics typically associated with high invasibility, namely isolation, high elevation, and location in the Pacific Ocean (van Kleunen et al. 2015; Pyšek et al. 2017; Essl et al. 2019). This suggests that the island is at an early stage of plant invasion and therefore remains highly susceptible to further establishment and spread of alien plants. In contrast, when compared with other eastern Pacific archipelagos, the naturalised-to-native ratio of Isla del Coco is close to those of Revillagigedo (0.40; Domínguez-Meneses et al. 2023) and Galapagos Archipelago (0.59; Guézou et al. 2010). While the low ratio in Revillagigedo could be linked to the absence of permanent human settlements until the late 1950s (Domínguez-Meneses et al. 2023), the moderate proportion of naturalised species in the Galapagos can respond to several factors, including the establishment of biosecurity protocols in 1999, and the strict land and biodiversity protection policy since late 1950s, that restrict human population to only 3% of the terrestrial land (Jimenez et al. 2024).

The taxonomic diversity of naturalised alien species is dominated by Cyperaceae and Poaceae. These families are well known for their weediness (Bryson and Carter 2008; Denslow et al. 2009; Lorence and Faccenda 2024), and their members would have been mostly unintentionally introduced in Isla del Coco as most of them have no use (63.2%). However, some Poaceae species may have been intentionally introduced as they are useful to animal feeding, such as *Megathyrus maximus*. Feral pigs (*Sus scrofa*) and domestic goats (*Capra hircus*) were intentionally introduced to the island in 1793 (Sierra 2001) and white-tailed deer (*Odocoileus virginianus*) in 1935 (Montoya 2016), likely facilitating the introduction of grasses (Poaceae) to support their grazing requirements (Montoya 2016). The introduc-

tion of alien grasses as forage to raise cattle is very well illustrated in the literature, including many parts of the Neotropics (Almeida et al. 2015; Overholt and Franck 2017) as well as in Pacific Islands (e.g., Hawaii; Faccenda 2025).

Among the alien species recorded on Isla del Coco, several spread rapidly, forming dense stands and displacing native vegetation, and are therefore classified in this study as invasive. These include *Calophyllum inophyllum*, *Coffea arabica*, *Megathyrus maximus*, *Terminalia catappa*, and *Urena lobata*. While some authors state that there are no strictly invasive plant species on Isla del Coco (Estrada-Chavarría et al. 2020), we believe that certain species warrant classification as invasive due to their apparent impact on native ecosystems, including observed pattern of abundance, ecological behavior, and potential for ecosystem disruption across invaded ranges (see Suppl. material 1). Unfortunately, there are no empirical studies of the impact of alien flora on ecosystems in Isla del Coco. In contrast, nearby oceanic archipelagos such as the Galapagos offer well-documented cases of invasive plant species causing aggressive competition, displacement of native taxa, and significant habitat alteration (e.g., Jäger et al. 2009, 2024; Rivas-Torres and Rivas 2018). This underscores the urgent need for field-based research on Isla del Coco to assess the ecological consequences of alien species and to confirm their invasion status. This need becomes even more pressing given that invasive mammal removal is on the near horizon (SINAC 2017), a measure that is likely to alter the dynamics and the composition of alien and native plant assemblages, as has been observed in other systems (see Vavra et al. 2007; Price et al. 2022; Vermeire et al. 2023). For instance, in the nearby Galapagos Islands, invasive *Rubus niveus* has become increasingly common in the highlands of Santiago Island, likely due to the release of herbivore pressure following the removal of introduced mammals (Carrion et al. 2011).

A major driver of the high alien-to-native ratio on Isla del Coco is the large proportion of casual alien species (53.9%), which contrasts with figures from other uninhabited islands like Revillagigedo (17.3%; Domínguez-Meneses et al. 2023), Saint Helena (20.8%; Lambdon and Darlow 2008), and Ascension (17.6%; Lambdon and Darlow 2008). The low percentage of casual species generally reported on oceanic islands is thought to result from limited field efforts targeting plant invasions, since the transient nature of casual taxa makes them easy to overlook (Herrera et al. 2025). This is probably why in the Galapagos Archipelago the percentage of casuals is substantially higher (65%; Guézou et al. 2010), as these islands have been the subject of numerous floristic surveys since many decades ago, including specific surveys for alien plants (Tye 2006). The relatively high percentage of casual flora on Isla del Coco is unlikely to reflect thorough floristic knowledge; instead, it more likely results from inadequate waste management prior to 2008. Notably, most casual species belong to the Fabaceae and Solanaceae families, both of which are highly significant in human food systems. During 2005–2008 the implementation of a compost treatment system for organic waste significantly reduced the propagule pressure of edible species (Madriz 2009), thereby lowering their chances of becoming naturalised. Propagule pressure is one of the main factors driving the establishment of alien taxa (Pyšek et al. 2010; Saccaggi et al. 2021; Vedder et al. 2021). The compost treatment system, along with several eradication actions that were carried out, is likely responsible for the local extinction of some casual alien species, including *Capsicum annuum*, *Cucumis sativus*, *Passiflora edulis* f. *flavicarpa*, *Psidium guajava* and *Solanum lycopersicum*. This highlights the importance of organic waste management on uninhabited islands, especially considering that some

of the alien casual species reported have demonstrated invasive potential on other islands. For example, *Psidium guajava* is one of the most invasive species in the nearby Galapagos Archipelago (Urquía et al. 2019).

The native range of alien species on Isla del Coco reveals a clear dominance of tropical taxa, reflecting strong environmental filtering, whereby species from non-tropical regions would face greater barriers to establishment due to climatic mismatches. This pattern aligns with findings from other oceanic islands. For example, Morente-López et al. (2023) found that climate matching is the dominant filter shaping alien floras in the Canary Islands, which, despite strong historical and trade connections to Mediterranean regions, host more tropical alien species. As precipitation is one of the most important variables driving plant invasions on tropical and subtropical islands (Irl et al. 2021), the more than 5000 mm of rainfall that Isla del Coco receives annually acts as a formidable environmental filter for alien species. Within the tropical realm, the predominance of Neotropical taxa in the alien flora of Isla del Coco is likely linked to the island's historical and contemporary ties to mainland Costa Rica. This regional bias in the native range of wild alien species is consistent with the growing body of literature demonstrating that patterns of alien species introduction and establishment closely follow the intensity and direction of trade flow networks (Seebens et al. 2015; Chapman et al. 2017; Hulme 2021).

In terms of growth forms, herbs and trees are the most prevalent among casual species, whereas herbs dominate among naturalised species in Isla del Coco. A similar pattern has been observed in the alien flora of Central America (Rojas-Sandoval et al. 2022), which is expected given that the alien flora of Isla del Coco likely represents a subset of Central America's native and alien flora (Trusty et al. 2006), mostly due to regular trade connections. The proportion of herbs among the naturalised species, however, is considerably higher in Isla del Coco (82.3%) than in Central America (60%; Rojas-Sandoval et al. 2022), contrary to the expectations. Globally, islands tend to host a lower proportion of herbaceous naturalised species compared to continental regions (Pyšek et al. 2017). The very high percentage of herbs in Isla del Coco could be attributed to the lack of long-term, sizable human settlements, which would have refrained from the massive introduction of ornamental plants (only 4.5% of the alien plants in Isla del Coco have exclusively ornamental uses), which are often characterised by presenting high proportions of woody species (e.g., Pergl et al. 2016; Ibáñez et al. 2023). Surprisingly, only a single herbaceous species has been recorded among the invasive taxa on Isla de Coco, which may be due to herbs' preference for trails and mowed areas and their tendency not to form dense stands that displace native vegetation on the island. Regarding the intentionality of alien species introductions, 61.8% have a documented use for humans, much lower than the 81% in the Galapagos Islands (Guézou et al. 2010). This discrepancy is, again, likely attributable to the uninhabited status of Isla del Coco.

We found no significant relationship between the global risk assessment categories and species invasion status categories, classified by expert criteria. Thus, the global risk assessment is clearly an inadequate tool for predicting invasions in Isla del Coco. While this approach can be useful for broad-scale risk assessments, it appears to be less effective when applied at a finer scale. In isolated ecosystems, where invasion dynamics may differ significantly from global patterns, expert-based evaluations tend to provide more accurate and context-sensitive assessments. Nevertheless, the global risk assessment remains a valuable tool for precautionary planning, especially in areas with limited ecological data or management capacity.

Site-based methods for inventorying alien species

Applying a binary decision-tree approach to determine species' native origin introduces several potential sources of error that warrant careful consideration. First, early alien introductions listed by Stewart (1912) may be erroneously categorised as native or cryptogenic (Q3). Relying on Stewart (1912) as a cornerstone reference for the native origin assessment is particularly problematic because it was published after major periods of human disturbance, including the establishment of the “Cocos Island Agricultural Company” in 1889. When comprehensive botanical surveys occur relatively late—as is common on uninhabited islands—they can help identify species recorded afterward as likely alien, but they provide limited evidence for determining whether earlier records represent true natives or early introductions. While previous authors (Trusty et al. 2006; Estrada-Chavarría et al. 2020) treated all species reported in Stewart (1912) as native, we introduced the cryptogenic category, which encompasses all ruderal species documented by Stewart (1912). Incorporating intermediate categories between alien and native allows us to explicitly acknowledge uncertainty and adopt a more conservative classification approach. Comparable multilevel classification systems have been applied in other island floras, such as the Galapagos Islands—where categories include ‘questionable accidental’, ‘questionable native’, and ‘questionable endemic’ (Guézou et al. 2017)—and the Canary Islands, which use ‘probable introduced’ and ‘probable native’ (Gobierno de Canarias 2025). The diversity of terms used for these intermediate categories across the aforementioned studies highlights the lack of standardisation in invasive plant terminology, an issue that is currently under debate (Soto et al. 2024). This inconsistency may hinder effective collaboration among scientists and limit engagement with policymakers, land managers or educators, ultimately leading to either over- or underestimation of invasion risks.

Second, some native species discovered after Stewart (1912) may be incorrectly classified as alien or cryptogenic due to their ruderal behaviour. Because Stewart's work is only semi-comprehensive and several species were documented subsequently, it is plausible that native ruderal species were overlooked. This problem is further exacerbated by the well-documented underrepresentation of large and taxonomically complex groups—such as Asteraceae, Poaceae, and Rubiaceae, many of which include ruderal species—in botanical surveys (Schmidt et al. 2025). In our decision tree, we use ruderal behaviour as an initial filter (Q4). However, we further refine the classification by distinguishing species that occur exclusively in ruderal habitats on Isla del Coco from those that occupy both ruderal and natural habitats (Q5). This two-step approach aims to reduce misclassification of native species that happen to exhibit ruderal tendencies.

Third, non-ruderal species are considered less likely to have been introduced—an assumption supported by evidence that alien species are strongly associated with human disturbance (Pyšek et al. 2010; van Kleunen et al. 2018). Nonetheless, the diversity of invasion syndromes across habitat types (Novoa et al. 2020) indicates that such an approach may overlook atypical introduction pathways. Despite this limitation, this compromise enables the identification of most alien species present on Isla del Coco. To address this issue, species that are neither ruderal nor useful for humans are classified as cryptogenic when both conditions evaluated in Q6 and Q7 are met simultaneously: their distribution must be restricted to areas near human settlements (i.e., the bays), and they must show no ecological association with bay

shore vegetation. These questions prevent supralittoral species that occur naturally in the bays from being misclassified as cryptogenic (e.g., *Conocarpus erectus*, *Dalbergia brownei*, *Mucuna sloanei*, and *M. urens*). This case illustrates how integrating knowledge of natural dynamics, human influences, and their interactions can help resolve context-specific classification challenges using binary decision rules.

Although our method accurately assessed whether most species are native, alien, or cryptogenic, we recognise that certain ambiguous cases (such as those described above) remain only partially resolved. Expert criteria can help identify species for which the decision tree may not perform reliably, thereby flagging cases that require additional scrutiny. For these species, targeted studies (such as population genetic analyses, biogeographic assessments, or detailed ecological surveys) would be necessary to confidently determine whether they are native to Isla del Coco.

Additionally, and unlike standard checklists, we consider it advisable to include species that no longer occur in Isla del Coco, i.e., those that have been subjected to eradication attempts. This approach allows us to build a useful database for ecological studies focused on invasion dynamics. Similarly, non-escaped cultivated species are often excluded from catalogues, and even escaped records of cultivated species are frequently overlooked by botanists (as, for instance, occurred in all floristic accounts of Galapagos till late 1980s; Tye 2006). Including them serves as a precautionary measure, establishing a historical precedent for their presence in case these species escape into the wild in the future.

Our assessment of the native origin of the spermatophyte flora of Isla del Coco differs from previous studies (Fig. 3) by Estrada-Chavarría et al. (2020) and Trusty et al. (2006) in the classification of a substantial number of species. On the one hand, 34 species (31.9% of the species previously classified as native) have changed their category when applying our site-based classification method. Specifically, 22 species shifted from native to cryptogenic (i.e., 20.1% of all species previously classified as native). Most of these are ruderal species recorded by Stewart (1912), while others were recorded after Stewart (1912) and exhibit ruderal behaviour elsewhere but not on Isla del Coco. In addition, 11 species (10.1%) shifted from being previously considered native to now being classified as alien. Some examples include species alien to the Neotropics whose cultural significance in introduced regions has sparked debate regarding their native status, such as *Calophyllum inophyllum* and *Cocos nucifera*. Others correspond to ruderal alien taxa recorded after Stewart's work (i.e., post-1912) that were previously classified as native, including *Desmodium incanum* or *Ipomoea tiliacea*. Finally, a single species previously reported as native has been reclassified as cultivated: *Plumeria rubra*, an ornamental species with no records of naturalisation.

On the other hand, 10 species (11.0% of the species previously classified as alien or cultivated) have changed their category. Two species shifted from alien to native, *Rhynchospora pubera* and *Scleria secans*, both of which are distributed beyond the northern bays of Isla del Coco and are not reported as ruderal elsewhere. Additionally, eight species shifted from alien to cryptogenic. Some of these exhibited ruderal behavior, even though they were recorded before Stewart (1912), while others display ruderal behaviour elsewhere but do not act as exclusively ruderal species on Isla del Coco. Additionally, our research documents 31 species not listed in the two previous studies: 15 cultivated species, 15 wild alien species, and one native species. The sole native species, *Scleria gaertneri*, is classified as native according to the decision tree applied in this study. This may be because the species has gone unnoticed until now, due to similarities with other congeneric species, although

this is unlikely. Alternatively, it may be that the species is not reported as ruderal in the consulted floras, or is one of those alien species without ruderal behaviour that our method does not address properly. Although our method classifies it as native, further research is needed to confirm this status. Given the inherent rigidity of this type of classification approach, it cannot be expected to apply flawlessly to all species, and in some cases, targeted studies will be required.

Conclusions and suggestions for management

Determining the species' native origin remains a global challenge, often constrained by inconsistent criteria and limited data. Although sole expert judgment has traditionally guided classifications, these approaches frequently lack transparency and reproducibility. The decision-tree framework developed in this study provides a structured, context-specific methodology for classifying species' native origin in specific areas, aligning with the principles of the 'ecology of place' and offering a model for data-limited regions—particularly in the Global South—where the management of biological invasions is often hindered by scarce resources. Applied to Isla del Coco, this approach revealed a higher proportion of wild alien spermatophytes (45.2%) compared to previous estimates.

From a conservation standpoint, the moderate proportion of alien species underscores the urgency of strengthening biosecurity measures in Isla del Coco, particularly those associated with trade and transport from the mainland. Regular and targeted botanical surveys focused on alien taxa are essential to enhance early detection and enable rapid response actions (Reaser et al. 2020). Future research should prioritise assessing the ecological impacts of invasive plants, clarifying the status of cryptogenic, and developing locally tailored risk assessment tools. Additionally, monitoring vegetation dynamics following the potential eradication of introduced mammals will be crucial for understanding post-restoration trajectories and guiding long-term conservation strategies on Isla del Coco. Furthermore, the next step is to investigate the native origin of pteridophytes, lycophytes, and bryophytes, as these groups remain understudied and may hold key insights into the island's alien flora.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: BO, LGA-V, JL-P, NN. Data curation: BO, LCVV. Formal analysis: BO, LCVV. Funding acquisition: BO, LCVV, LGA-V. Investigation: BO, LCVV. Methodology: BO, LGA-V, JL-P, NN. Project administration: LGA-V. Resources: JPM-M. Supervision: JP, JAC, NN, JL-P. Writing - original draft: BO, LCVV, NN, JL-P. Writing - review and editing: All authors.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Invasive alien plant species of Isla del Coco, Costa Rica

Authors: Beñat Orbea, Luis Carlos Vega Vargas, Jairo Patiño, Juan Antonio Campos, Luis Guillermo Acosta-Vargas, Neus Nualart, José Pablo Madriz-Masis, Jordi López-Pujol

Data type: pdf

Explanation note: Information on the process of introduction on the island and effects on the natural ecosystems are provided.

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Link: <https://doi.org/10.3897/neobiota.106.168397.suppl1>

Supplementary material 2

Inventory of wild alien plant species for Isla del Coco, Costa Rica

Authors: Beñat Orbea, Luis Carlos Vega Vargas, Jairo Patiño, Juan Antonio Campos, Luis Guillermo Acosta-Vargas, Neus Nualart, José Pablo Madriz-Masis, Jordi López-Pujol

Data type: docx

Explanation note: Inventory of wild alien plant species for Isla del Coco, Costa Rica, including information on invasion status, putative origin, life-history traits, uses, distribution and abundance, global risk and the previous origin classification status of Trusty et al. (2006) and Estrada-Chavarría et al. (2020).

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Supplementary material 3

Decision tree responses

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Data type: xlsx

Explanation note: Complete set of responses generated by the decision tree for all species evaluated.

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Supplementary material 4

Inventory of crops for Isla del Coco, Costa Rica

Authors: Beñat Orbea, Luis Carlos Vega Vargas, Jairo Patiño, Juan Antonio Campos, Luis Guillermo Acosta-Vargas, Neus Nualart, José Pablo Madriz-Masis, Jordi López-Pujol

Data type: docx

Explanation note: Inventory of crops for Isla del Coco, Costa Rica, including information on putative origin, cultivation state, life-history traits, uses, and global risk.

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